Tree Physiology 19, 871–878

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Foliar temperature–respiration response functions for broad-leaved tree species in the southern Appalachians

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Received August 11, 1998

Summary We measured leaf respiration in 18 eastern deciduous forest tree species to determine if there were differences in temperature–respiration response functions among species or among canopy positions. Leaf respiration rates were measured *in situ* and on detached branches for *Acer pensylvanicum* L., *A. rubrum* L., *Betula* spp. (*B. alleghaniensis* Britt. and *B. lenta* L.), *Carya glabra* (Mill.) Sweet, *Cornus florida* L., *Fraxinus* spp. (primarily *F. americana* L.), *Liriodendron tulipifera* L., *Magnolia fraseri* Walt., *Nyssa sylvatica* Marsh., *Oxydendrum arboreum* L., *Platanus occidentalis* L., *Quercus alba* L., *Q. coccinea* Muenchh., *Q. prinus* L., *Q. rubra* L., *Rhododendron maximum* L., *Robinia psuedoacacia* L., and *Tilia americana* L. in the southern Appalachian Mountains, USA. Dark respiration was measured on fully expanded leaves at 10, 15, 20, 25, and 30 °C with an infrared gas analyzer equipped with a temperature-controlled cuvette. Temperature–respiration response functions were fit for each leaf. There were significant differences in response functions among species and by canopy position within species. These differences were observed when respiration was expressed on a mass, nitrogen, or area basis. Cumulative nighttime leaf respiration was calculated and averaged over ten randomly selected nights for each leaf. Differences in mean cumulative nighttime respiration were statistically significant among canopy positions and species. We conclude that effects of canopy position and species on temperature–respiration response functions may need to be considered when making estimates of whole-tree or canopy respiration.

Keywords: broad-leaved trees, canopy position, leaf respiration, Q_{10}.

Introduction

Leaf respiration is a substantial component of total respiration in many ecosystems (Amthor 1989, Paembonan et al. 1991, Ryan 1991, Yokota and Hagihara 1995). Respiration is an essential process for the construction of new tissue (R_g) and for the maintenance of existing tissue (R_m); for example, in membrane repair, ion transport, and enzyme resynthesis and transport (Merino et al. 1982, Amthor 1984, Ryan 1991). The main factors controlling leaf respiration rates include temperature, tissue nitrogen content, time of year (growth and maintenance components), species, population, and genotype (Mooney 1963, Lawrence and Oechel 1983, Criddle et al. 1994, Tjoelker et al. 1995).

Exponential response functions may be used to predict R_m as a function of temperature (Landsberg 1986, Amthor 1989). One common form is

$$R_m = R_{T_{ref}} Q_{10} \frac{(T - T_{ref})}{10}, \quad (1)$$

where $R_{T_{ref}}$ is an estimate of R_m at the reference temperature T_{ref}, and Q_{10} quantifies the shape of the temperature–respiration response function. Parameter Q_{10} is defined as the ratio of respiration at a given temperature divided by respiration at a temperature 10 degrees lower, so a larger Q_{10} signifies a larger proportional change in respiration rate with a 10 degree change in temperature. The parameters of Equation 1 are best estimated by regression when more than two respiration measurements are made, and Q_{10} is estimated across the measured temperature range.

General models in the form of Equation 1 entail several assumptions. First, it is assumed that the fit coefficients are appropriate over the entire temperature range of interest, and that they do not change with other factors, e.g., tissue nitrogen content, population, or species. If these assumptions are not valid, then individual models may need to be fit for each group, or the models need to be modified to incorporate these differences. Numerous studies have shown a linear relationship between respiration and tissue nitrogen content (Amthor 1989, Ryan 1991), because a large proportion of tissue nitrogen is incorporated in proteins, and a correspondingly large proportion of maintenance respiration is used during protein resynthesis and repair. Furthermore, these relationships are valid across a number of species (Ryan 1995, Reich et al. 1998). However, several factors may cause variation in respiration–N relationships, including differences in enzyme turnover rates, concentrations of secondary metabolic products, and differences in structural–functional nitrogen proportions.

A second assumption in Equation 1 is that the parameters do not vary with temperature; i.e., that $R_{T_{ref}}$ and Q_{10} are constant across the temperature range of interest for the target population of leaves. Although Q_{10} has been reported to change little

for a range of temperate species (Lyons and Raison 1970), other work indicates that Q_{10} varies with species, subspecies, and growth temperature (Raison 1980, Reich et al. 1998). Because there have been relatively few studies on leaf respiration in deciduous forest tree species, the reason for this discrepancy has not been elucidated. Parameters for temperature–respiration response functions (Equation 1) are unknown for most tree taxa, and we particularly lack knowledge on how these functions vary among species, by canopy position (and hence leaf light environment), nitrogen content, and other conditions (Amthor 1989). This lack of knowledge causes substantial uncertainty in estimates and models of productivity and carbon flux and balances at whole-plant, stand, landscape, and global scales. Our study objectives were to estimate typical foliar temperature–respiration response functions for dominant southern Appalachian tree species, and to determine if these functions differ by species and canopy position within species. We also estimated the net effects of these differences on cumulative nighttime leaf respiration in an eastern deciduous broadleaf forest.

Methods

Dark respiration rates of leaves were measured on trees growing in and near the Coweeta Hydrologic Laboratory (35°3′ N, 83°25′ W), in the southern Appalachian Mountains, USA. A total of 428 leaves were sampled, representing 18 broad-leaved woody tree species, from approximately 300 to 1500 m elevation. Sampling focused on mature individuals (30 to 110 years) of the dominant tree taxa. Upper canopy (High or H) leaves, which were selected from the top of canopy dominants or on the outer edge of forest edge trees, were all exposed to at least half of the open sky hemisphere. These leaves would receive direct sunlight for at least half of a sunny day. Canopy bottom (Low or L) leaves, which were selected from near the bottom of interior forest trees in mature closed-canopy stands, received little direct sunlight. Mid-canopy (Middle or M) leaves were typically selected from the middle third of the canopy but not the outermost leaves. Leaves were accessed from permanent and temporary towers and with pole pruners. Foliar R_m was measured with an infrared gas analyzer (LCA3, Analytical Development Corp., Hoddesdon, England) equipped with a temperature-controlled cuvette (Pearcy et al. 1989, Hubbard et al. 1995). Flux of CO_2 was measured at 10, 15, 20, 25, and 30°C (± 0.1 °C). Equivalence of measurements of respiration on leaves *in situ* versus leaf respiration of cut branches was established by means of a series of paired measurements (see Mitchell et al. 1999 for further details of sampling).

Temperature–respiration response functions (Equation 1) were fit for each leaf by nonlinear regression, with respiration expressed on a per unit mass (R_{mass}; μmol CO_2 (kg leaf dry mass)$^{-1}$ s^{-1}), per unit nitrogen (R_N; μmol CO_2 (kg leaf N)$^{-1}$ s^{-1}), and per unit leaf area (R_A; μmol CO_2 m^{-2} s^{-1}) basis. For all models, $R_{T_{ref}}$ was set to 20 °C. Respiration functions were fit on all three bases to facilitate comparisons with previous work (Mooney 1963, Mooney et al. 1964, Ryan 1991, 1995, Villar et al. 1995, Yokota and Hagihara 1995, Reich et al. 1996). Residual behavior was examined with normal plots and Komolgorov-Smirnov tests. Cook's D tests were used to identify outliers, and Pearson's correlation coefficients were calculated for Q_{10}–$R_{T_{ref}}$ pairs. Residual analyses flagged individual respiration–temperature measurements as extreme outliers in seven of the 428 leaves, and these were dropped from subsequent analyses. The Q_{10}–$R_{T_{ref}}$ pairs covaried, thus statistical comparisons within and among species required the multivariate pair be considered together. Significance differences among curves were identified by appropriate Wilk's Λ tests (Johnson and Wichern 1982). In the event of significant Wilk's Λ, Duncan's new multiple-range tests (NMRT) were used to identify differences among $R_{T_{ref}}$ and Q_{10} within and among species (Chew 1977). Parameters were regressed against leaf nitrogen for all data and for subsets grouped by canopy position and species. Once coefficients for leaf temperature–respiration functions were estimated, cumulative nighttime leaf respiration was calculated for each sampled leaf, based on measured meteorological data and fitted N-based temperature–respiration response functions. Hourly temperature data were collected at five meteorological stations spanning the range of elevations and slope positions at the Coweeta Hydrologic Laboratory (Swift et al. 1988). These data were used with a locally developed and validated landscape temperature prediction model (Bolstad et al. 1998) to estimate canopy temperatures for each second on each of 10 randomly selected nights (Julian days 168, 174, 184, 191, 201, 209, 223, 228, 241 and 245) during the 1994 growing season. Temperature data were used with individual leaf temperature–respiration response functions to predict leaf respiration for each second of each night. Cumulative nighttime respiration was then summed for each leaf, and averaged by canopy position. The relationships between R_m, canopy position, nitrogen, and elevation were then tested in a series of ANOVAs and regression analyses.

Results and discussion

Temperature–respiration response functions

Estimated temperature–respiration response functions, based on Equation 1, fit the individual leaf data well. Mean and minimum regression R^2 values were 0.96 and 0.89, respectively, for the 421 fitted leaf temperature–respiration response functions. Equation 1 parameters covaried, with $R_{T_{ref}}$–Q_{10} covariances of −0.25, −0.14, and −0.36, respectively for mass-, nitrogen-, and area-based models. This covariance indicates that higher Q_{10} values tend to occur at lower $R_{T_{ref}}$ values. We report parameters for respiration expressed on mass, N, and area bases (Table 1) to facilitate comparison with published reports, and because the most useful form in future studies will depend on the question and context. Correlations among $R_{T_{ref}}$–Q_{10} parameters were significant for all model forms ($P < 0.05$, *t*-test), indicating that significance tests should be conducted on fit pairs (Johnson and Wichern 1982).

Mean Q_{10} was the same within most species and canopy positions when estimated on a mass, nitrogen, or an area basis ($P < 0.05$ for within-species comparisons, NMRT). Values of Q_{10} differed among the three bases ($P < 0.05$, GLM and

Table 1. Equation 1 coefficients (and SE), by species and canopy position. Values of Q_{10} did not vary significantly when fit on a mass and nitrogen basis. Models were fit by using nonlinear regression of the form $R = R_{T_{ref}} Q_{10}(T - T_{ref})/10$, $T_{ref} = 20$ °C. Abbreviations: H = upper canopy leaves, L = lower canopy leaves, and M = intermediate canopy leaves. See text for description of canopy position.

Taxa	Canopy position	$R_{T_{ref}}$, mass μmol (kg leaf)$^{-1}$ s^{-1}	$R_{T_{ref}}$, nitrogen μmol (kg N)$^{-1}$ s^{-1}	$R_{T_{ref}}$, area μmol (m leaf)$^{-2}$ s^{-1}	Q_{10}	n
Acer rubrum	H	6.23 (0.36)	349 (17.9)	0.506 (0.046)	2.47 (0.17)	8
	M	6.36 (0.32)	332 (18.5)	0.467 (0.024)	2.33 (0.05)	21
	L	5.62 (0.118)	313 (7.74)	0.285 (0.032)	2.70 (0.07)	8
Betula spp.	H	8.27 (0.43)	444 (29.1)	0.540 (0.029)	2.6 (0.11)	10
	M	7.91 (0.39)	376 (31.5)	0.357 (0.037)	2.59 (0.11)	8
	L	6.06 (0.45)	284 (24.4)	0.229 (0.025)	2.94 (0.12)	9
Carya glabra	H	6.11 (0.11)	250 (14.6)	0.518 (0.031)	2.40 (0.11)	10
	M	5.41 (0.06)	244 (14.1)	0.425 (0.024)	2.48 (0.06)	11
	L	5.29 (0.43)	239 (19.9)	0.271 (0.029)	2.53 (0.11)	13
Liriodendron tulipifera	H	8.09 (0.04)	407 (50.2)	0.621 (0.058)	2.23 (0.04)	8
	M	7.10 (0.37)	291 (19.1)	0.363 (0.032)	2.15 (0.05)	6
	L	6.58 (0.22)	284 (16.8)	0.315 (0.023)	2.21 (0.04)	10
Quercus alba	H	8.02 (0.66)	341 (12.3)	0.773 (0.045)	2.20 (0.03)	15
	M	6.87 (0.40)	293 (12.2)	0.405 (0.032)	2.25 (0.05)	18
	L	7.82 (0.45)	337 (17.0)	0.501 (0.043)	2.17 (0.04)	13
Quercus coccinea	H	5.24 (0.28)	275 (17.5)	0.563 (0.046)	2.29 (0.10)	8
	M	3.82 (0.12)	206 (29.4)	0.387 (0.046)	2.46 (0.08)	7
	L	4.09 (0.21)	193 (8.02)	0.299 (0.022)	2.42 (0.10)	8
Quercus prinus	H	8.12 (0.56)	343 (24.7)	0.911 (0.061)	2.31 (0.10)	12
	M	6.92 (0.27)	250 (13.4)	0.480 (0.071)	2.32 (0.05)	4
	L	8.54 (0.55)	358 (22.5)	0.448 (0.031)	2.34 (0.05)	12
Quercus rubra	H	7.49 (0.48)	264 (14.1)	0.724 (0.047)	2.28 (0.04)	6
	M	5.75 (0.30)	248 (9.5)	0.415 (0.070)	2.38 (0.08)	9
	L	4.91 (0.41)	185 (5.8)	0.281 (0.032)	2.55 (0.08)	8
Acer pensylvanicum	M	7.26 (0.31)	372 (23.8)	0.283 (0.013)	2.48 (0.11)	6
	L	5.47 (0.36)	297 (16.2)	0.187 (0.014)	2.76 (0.12)	8
Cornus florida	H	7.17 (0.43)	416 (41.3)	0.482 (0.013)	2.44 (0.09)	4
	M	7.51 (0.37)	510 (66.4)	0.428 (0.060)	2.71 (0.17)	4
	L	7.91 (1.08)	404 (45.8)	0.312 (0.053)	2.68 (0.13)	3
Fraxinus spp.	H	7.49 (0.43)	401 (51.8)	0.655 (0.129)	2.21 (0.08)	4
	M	6.34 (0.40)	307 (18.2)	0.357 (0.043)	2.62 (0.09)	6
	L	6.71 (0.50)	370 (52.5)	0.413 (0.048)	2.35 (0.09)	8
Magnolia fraseri	H	6.83 (0.82)	297 (31.7)	0.340 (0.086)	2.10 (0.13)	4
	M	7.31 (0.78)	324 (17.9)	0.375 (0.022)	2.10 (0.09)	3
	L	5.48 (0.98)	234 (44.5)	0.192 (0.037)	2.48 (0.27)	4
Nyssa sylvatica	M	6.89 (0.39)	360 (30.3)	0.342 (0.021)	2.44 (0.11)	5
	L	6.85 (0.63)	401 (36.4)	0.314 (0.035)	2.29 (0.05)	5
Oxydendrum arboreum	H	7.30 (0.21)	394 (13.7)	0.278 (0.009)	2.65 (0.16)	2
	M	5.31 (0.33)	267 (11.5)	0.247 (0.026)	3.15 (0.27)	6
	L	5.84 (0.83)	370 (54.6)	0.223 (0.036)	3.02 (0.16)	6
Platanus occidentalis	H	5.03 (0.01)	243 (3.8)	0.345 (0.004)	2.32 (0.04)	2
	M	5.73 (0.53)	333 (36.9)	0.335 (0.036)	2.10 (0.05)	4
	L	5.63 (0.35)	321 (11.4)	0.274 (0.025)	2.23 (0.05)	6
Rhododendron maximum	M	1.97 (0.06)	180 (7.0)	0.202 (0.004)	2.32 (0.03)	4
	L	1.55 (0.04)	149 (4.1)	0.177 (0.020)	2.84 (0.27)	3
Robinia pseudoacacia	H	7.37 (0.61)	241 (30.5)	0.565 (0.060)	2.39 (0.03)	3
	M	6.50 (0.63)	177 (13.3)	0.381 (0.013)	2.49 (0.04)	4
	L	9.79 (0.28)	278 (12.3)	0.469 (0.048)	2.69 (0.15)	3
Tilia americana	H	6.73 (0.55)	233 (10.5)	0.462 (0.035)	2.28 (0.07)	5
	M	6.27 (0.79)	225 (9.1)	0.325 (0.030)	2.34 (0.02)	3
	L	6.80 (0.54)	248 (10.8)	0.266 (0.046)	2.34 (0.12)	4

Wilk's Λ) for only nine of 51 species–canopy combinations. We conclude that the temperature–respiration response functions do not fundamentally change shape within species and canopy position, but rather are scaled when respiration is expressed on a leaf mass, N, or area basis, and this scaling difference is largely reflected in the $R_{T_{ref}}$ parameter.

Canopy position

Temperature–respiration response functions differed by leaf canopy position for approximately 50% of the species (Table 1), indicating that canopy position, and by inference, leaf light environment, is an important factor influencing temperature–respiration response functions ($P < 0.05$, Wilk's Λ). Leaves in the upper canopy typically had significantly higher dark respiration rates than leaves in the lower canopy whether respiration was expressed on a mass, area, or nitrogen basis (Table 1). Furthermore, this difference was often maintained across the entire range of tested temperatures (Figure 1). Mass- and nitrogen-based temperature–respiration curves differed significantly among canopy positions for five of the eight well-sampled species ($P < 0.05$, GLM and Wilk's Λ, *Q. rubra*, *Q. coccinea*, *Q. prinus*, *L. tulipifera*, *Betula* spp., whereas $P > 0.05$ for *A. rubrum*, *Q. alba*, *C. glabra*). Different canopy positions had significantly different area-based respiration functions within all eight well-sampled species. Sample sizes were notably smaller for ten of the eighteen species, with two to four leaves sampled at several canopy positions, which was probably too few to provide sufficient statistical power for testing differences among responses. Of these species, only *A. pensylvanicum* showed significant effects of canopy position on mass- and N-based respiration, and eight of 10 species showed significant effects of canopy position on area-based temperature–respiration response functions.

Changes in $R_{T_{ref}}$ were largely responsible for the differences in respiration with canopy position. Values of $R_{T_{ref}}$ typically decreased with lower canopy positions, whereas Q_{10} showed a variable pattern, with a slight tendency to increase down the canopy. Values of Q_{10} were significantly affected by canopy position in only one of the eight well-sampled species, whereas $R_{T_{ref}}$ values differed significantly in five (mass- and N-based) to eight (area-based) of the well-sampled species ($P < 0.05$, Duncan's NMRT). When other factors are held constant, a decrease in $R_{T_{ref}}$ corresponds to a lower respiration rate at a given temperature, and an increase in Q_{10} corresponds to larger changes in respiration rate with a 10 °C change in temperature. Because $R_{T_{ref}}$ decreased and Q_{10} often increased at lower canopy positions, the overall impact of canopy position, and hence light environment, on temperature–respiration functions is not directly apparent. However, substituting the parameters from Table 1 into Equation 1 shows a net decrease in respiration for low-canopy leaves relative to upper-canopy leaves for most of our well-sampled species (Figure 1). This net decrease occurs whether respiration is expressed on mass, nitrogen, or area basis. Upper-canopy leaves had higher respiration rates than canopy-bottom leaves over our 10 to 30 °C temperature range for six of eight species. Temperature–respiration response curves for mid-canopy leaves (not shown) typically fell between those of the upper and lower canopy over the tested temperature range.

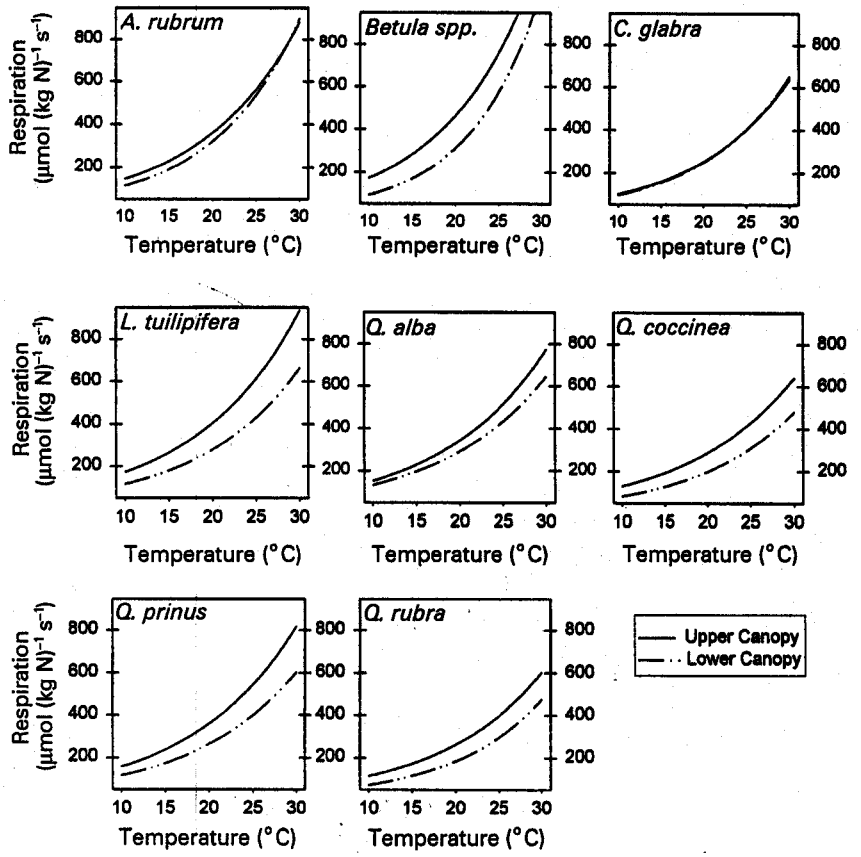

Figure 1. Temperature–respiration response functions, nitrogen basis, for the eight well-sampled species. Curves are based on the mean Equation 1 coefficients fit from 6 to 15 leaves, with T_{ref} at 20 °C. Upper canopy leaves were near or at the top of the forest canopy and exposed to direct sunlight for more than half of sunny mid-summer days. Lower canopy leaves were near the bottom of the canopy in closed forests and exposed to little or no direct sunlight during sunny mid-summer days. High versus low canopy response functions were statistically different (Wilk's Λ, $P < 0.05$), for *Betula* spp., *Liriodendron tulipifera*, *Quercus coccinea*, *Q. rubra* and *Q. prinus*.

The differences in temperature–respiration response functions among canopy positions are notable for several reasons. First, scaling by nitrogen to estimate whole-tree or canopy respiration (Ryan 1995, Reich et al. 1996, 1998) would become more complicated. We found similar N concentrations in the upper and lower canopy, but nitrogen-based respiration rates still differed among canopy positions. Leaf internal and external morphology change in response to light environment, and these changes may alter leaf structure, chlorophyll quantity, leaf chemistry and the proportion of structural and metabolic nitrogen (Givnish 1988, Evans 1989). Realized photosynthetic rates are generally higher in sun leaves than in shade leaves, and conversion, transport, repair, or other requirements associated with assimilating higher quantities of fixed carbon may be the cause of high mass- and nitrogen-based respiration rates of upper-canopy leaves. Upper- and lower-canopy leaves are reported to have similar nitrogen and enzyme concentrations (McMillen and McClendon 1983, Reich et al. 1998), so we doubt that the observed higher respiration rates are caused directly by increased enzyme synthesis. The higher metabolic costs per unit N in the upper canopy may be associated with increased carbohydrate concentrations and processing. Dark respiration rates change with rates of photosynthesis in the previous period, and may be related to net C assimilation (McCree 1974, Azcón-Bieto and Osmond 1983).

The observed effects of canopy position on temperature–respiration response functions are also of interest because they occurred across a number of common species, and did not appear to be consistent across genera or shade tolerance. The two instances where upper- and lower-canopy functions were most similar were for the most shade tolerant of our well-sampled species, *Acer rubrum* and *Carya glabra*. The most shade-intolerant species, *Liriodendron tulipifera*, showed one of the largest differences in upper- versus lower-canopy leaf temperature–respiration response functions. Differences may reflect among-species differences in acclimation to light environments. However, we consider that our results provide only weak evidence of light acclimation as a cause of the differences, because taxa intermediate in shade tolerance had among the highest (*Betula* spp.) and lowest (*Quercus rubra*) differentials in upper canopy versus lower canopy leaf respiration rates.

Species effects

Temperature–respiration response functions differed among species ($P < 0.05$, Wilk's Λ). There were no distinct groupings of species, and differences were a result of differences in $R_{T_{ref}}$. Values of Q_{10} rarely differed among species ($P > 0.05$, NMRT). Among-species comparisons indicated that *Carya glabra*, *Quercus coccinea*, *Betula* spp., *Acer rubrum* and *Platanus occidentalis* had significantly lower $R_{T_{ref}}$ on a mass basis than most other overstory species at corresponding light environments, whereas *Quercus prinus*, *Quercus alba*, *Liriodendron tulipifera*, and *Magnolia fraseri* had higher $R_{T_{ref}}$ on a mass basis ($P < 0.05$, Duncan's NMRT). Values of $R_{T_{ref}}$ on mass and area bases were notably low for *Oxydendrum arboreum*, *Nyssa sylvatica*, *Cornus florida*, and particularly for *Rhododendron maximum*, the only non-deciduous species sampled. The low values of $R_{T_{ref}}$ for *Rhododendron maximum* are consistent with reported general relationships among leaf respiration, nitrogen, life span, and other leaf traits (Reich et al. 1998). Similar groupings were observed when respiration was expressed on a unit nitrogen basis, although there were fewer significant differences in paired comparisons of $R_{T_{ref}}$ on a nitrogen basis ($P < 0.05$, NMRT). *Robinia pseudoacaccia*, a nitrogen fixer, showed a significant change in rank-order of $R_{T_{ref}}$ (nitrogen basis) relative to $R_{T_{ref}}$ (mass basis). Low respiration rates per unit nitrogen perhaps reflect increased non-enzymatic N, and low metabolic activity per unit nitrogen for this species.

Nitrogen effects

Values of $R_{T_{ref}}$ on a mass basis were significantly related to leaf N content ($P < 0.05$, linear regression, pooled data), indicating respiration per unit mass at any given temperature increased with increasing leaf nitrogen content. Values of Q_{10} were not significantly related to leaf N content in linear regressions.

Significant differences within or among species in respiration–temperature or respiration–nitrogen relationships may complicate estimates of whole-canopy respiration. One method of scaling respiration estimates from leaves to canopies involves expressing respiration on a mass nitrogen basis. If respiration is tightly linked with nitrogen per unit mass, measurements of tissue nitrogen content and temperature could be used to obtain accurate estimates of component respiration flux. Nitrogen per unit mass has been shown to remain fairly constant vertically through the canopy (Jurik 1986, Ellsworth and Reich 1993, Mitchell et al. 1999), and other work has established a strong relationship between mass-based nitrogen and mass-based respiration (Ryan 1991, 1995). However, although we found similar nitrogen content per unit mass in all three of our canopy position categories, we also found significant differences in nitrogen-based temperature response functions among species and canopy positions. Whole-canopy respiration is a function of several factors, including leaf respiration rates, leaf biomass, and woody biomass and respiration rates. Although these other factors may be more important in determining total canopy respiration, our individual leaf measurements suggest that species and canopy position differences in temperature–respiration response may also impact whole-canopy respiration, even though leaf nitrogen and temperature regimes may be identical. We believe general N-based scaling of canopy respiration should be tested further with specific functions fit from measurements in a partitioned canopy.

Cumulative nighttime respiration

Mean cumulative nighttime mass- and nitrogen-based respiration varied significantly by canopy position with our pooled all-species data, at least when averaged over the 10 randomly chosen nights (Table 2, $P < 0.05$, ANOVA). Within-species mass- and nitrogen-based total respiration varied significantly among canopy position for a subset of species (Table 3,

Table 2. Mean (and SE) respiration rates by canopy position for 10 randomly selected growing season nights, including those species measured at all three canopy positions.

Canopy position	R_{mass} (mol CO_2 (kg leaf)$^{-1}$ night^{-1})	R_N (mol CO_2 (kg N)$^{-1}$ night^{-1})	Elevation (m)	Mean 10-night temperature (°C)	Leaf N (mg g^{-1})	Number of leaves
H	0.2103 (0.0041)	9.52 (0.22)	954 (33.1)	21.7 (0.146)	22 (0.5)	102
M	0.1711 (0.0027)	8.16 (0.18)	852 (32.0)	22.1 (0.142)	22 (0.5)	131
L	0.1671 (0.0062)	8.78 (0.19)	906 (25.6)	21.8 (0.108)	22 (0.4)	141

Table 3. Mean (and SE) for nighttime leaf respiration, based on 10 nights randomly selected from the 1994 growing season.

Taxa	Canopy position	R_{mass} (mol CO_2 (kg leaf)$^{-1}$ night^{-1})	Mean 5-night temperature (°C)	Mean leaf N (mg g^{-1})	*n*
Acer rubrum	H	0.175 (0.011)	20.1 (0.6)	19 (1)	8
	L	0.156 (0.010)	20.9 (0.4)	19 (1)	8
Betula spp.	H	0.230 (0.014)	21.5 (0.3)	22 (1)	10
	L	0.167 (0.012)	21.8 (0.4)	22 (1)	9
Carya glabra	H	0.172 (0.011)	21.8 (0.5)	23 (2)	10
	L	0.148 (0.009)	21.7 (0.5)	21 (2)	13
Liriodendron tulipifera	H	0.229 (0.014)	22.3 (0.1)	25 (1)	8
	L	0.186 (0.010)	22.1 (0.2)	23 (1)	10
Quercus alba	H	0.225 (0.012)	22.2 (0.5)	24 (1)	15
	L	0.222 (0.011)	22.2 (0.5)	19 (1)	13
Quercus coccinea	H	0.148 (0.009)	22.3 (0.1)	20 (2)	8
	L	0.115 (0.007)	22.8 (0.4)	21 (1)	8
Quercus prinus	H	0.230 (0.013)	20.3 (0.2)	28 (1)	12
	L	0.240 (0.013)	21.4 (0.3)	29 (2)	12
Quercus rubra	H	0.211 (0.015)	19.6 (0.3)	24 (2)	6
	L	0.137 (0.010)	21.0 (0.6)	23 (2)	8

ANOVA, $P < 0.05$, individual species canopy position comparisons for all but *Cornus florida*, *Fraxinus* spp., *Nyssa sylvatica*, *Quercus alba*, and *Tilia americana*). Among-species differences in cumulative nighttime respiration were significant; however comparisons among species must be made with care because of differences in species distribution and the elevations at which each species was sampled. For example, calculated cumulative nighttime respiration for *Quercus rubra* and other high-elevation species were typically lower than those for *Liriodendron tulipifera*, in part because lower temperatures prevail at the higher elevations where *Quercus rubra* is found. However, when subsets of samples were chosen to balance the elevation sampling range, many among-species comparisons showed significant differences in cumulative respiration (e.g., *Acer rubrum* versus *Quercus alba*, $P < 0.05$, NMRT). Cumulative nighttime respiration typically decreased with canopy position when samples were from similar elevations, particularly when sample sizes were greater than six leaves per species for both upper- and lower-canopy positions.

Mean cumulative nighttime respiration decreased with elevation whether it was expressed on a mass or nitrogen basis (Figures 2a and 2b). These relationships were significant for

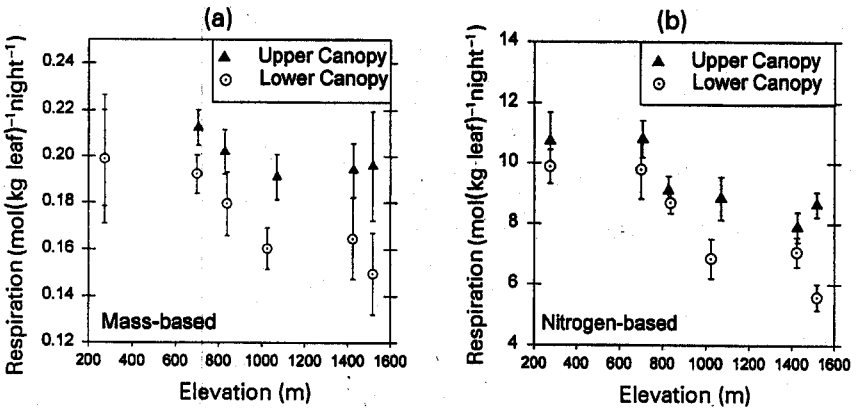

Figure 2. Mass-based (a) and nitrogen-based (b) respiration versus elevation for the eight most common canopy species (*Acer rubrum*, *Betula* spp., *Carya glabra*, *Liriodendron tulipifera*, *Quercus rubra*, *Q. cocinea*, *Q. prinus*, *Q. alba*). Both mass- and nitrogen-based respiration decreased with elevation in response to lower temperatures at higher elevations. Nitrogen-based respiration decreased more steeply, reflecting the elevational increase in leaf nitrogen content.

the pooled data, and all canopy subsets except the upper canopy, mass-based respiration ($P < 0.05$, regression slope). Nitrogen-based respiration decreased more rapidly than mass-based respiration with increasing elevation. This is primarily because tissue nitrogen content increased with elevation (Mitchell et al. 1999). Higher respiration at a fixed temperature is a frequently noted adaptation/acclimation response in plants grown in cool environments (Larigauderie and Körner 1995). Acclimation may manifest itself in higher nitrogen per unit mass at higher elevations, leading to higher respiration per unit mass at any given temperature. Complete acclimation/adaptation would result in equivalent mass-based respiration across the range of temperatures. Although our data suggest some acclimation/adaptation may have occurred, it was not complete because cumulative respiration decreased with elevation (Figures 2a and 2b).

Conclusions

We observed temperature–respiration response functions for 18 broad-leaved forest tree species common in the southern Appalachians of North America. Temperature–respiration response functions varied significantly by canopy position both within species and for data pooled across species, and corresponding temperature–respiration response functions also varied significantly by canopy position within and among species. Because Q_{10} showed no distinct trend, we conclude that Q_{10} did not vary by canopy position and only occasionally varied among the species we tested. Most of the differences among species or among canopy positions appeared to be the result of differences in $R_{T_{ref}}$. Differences in temperature–respiration response functions occurred whether expressed on a mass, area, or nitrogen basis, indicating that simple scaling based on nitrogen or mass may not be appropriate. Our data indicate that differences in species and the distribution of leaf light environments may significantly alter cumulative nighttime leaf respiration, even when expressed on a unit nitrogen basis, and we conclude that these factors should be considered when estimating leaf respiration at canopy or broader scales.

Acknowledgments

Funding for this research was provided by NSF grants DEB-9596191 and BSR-9011661 and by the Minnesota Agricultural Experiment Station. We thank Charles Marshall for field support, and M. Ryan, M. Tjoelker, and P. Reich for helpful comments on this paper.

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